

Does the platypus have a stomach? The perils of popular science

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ABSTRACT

If you search the internet for platypus stomach you will find countless websites stating that the platypus has no stomach. Some also state that echidnas also have no stomach. But platypuses and echidnas do have stomachs, although they differ from the stomachs of all other mammals by being non-secretory. In this paper I review the history of anatomical descriptions of monotreme stomachs, discuss the functions of the stomach in vertebrates, and show how the absence of acid secretion has been confused with absence of a stomach. The misunderstanding and misrepresentation of platypus anatomy and physiology provides an interesting example of how science misinformation can be propagated.

Key words: *Ornithorhynchus anatinus*; *Tachyglossus aculeatus*; gastric acid; Everard Home, cheek pouches

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Introduction

In 2013 National Geographic published an on-line story titled “How the Platypus and a Quarter of Fishes Lost Their Stomachs”: “*The platypus is an anthology of weirdness. It has a leathery duck-like bill, a flattened tail and webbed feet. The males have a venomous claw on their hind feet, and the females lay eggs. And if you look inside a platypus, you’ll find another weird feature: its gullet connects directly to its intestines. There’s no sac in the middle that secrete powerful acids and digestive enzymes. In other words, the platypus has no stomach*” (Yong, 2013). This was picked up and echoed across the internet. The Smithsonian Magazine wrote “... platypuses, spiny echidnas and around 25 percent of fish species are among those animals that have returned to a pre-stomach state.” (Nuwer, 2013) and a University of Melbourne webpage states that the platypus has “an oesophagus that connects directly with the intestine” (op den Brouw, 2020). A frequent ingredient of the seemingly inevitable description of echidnas and platypuses as weird is the claim that they do not have stomachs, and the National Geographic article is one of many. But echidnas and platypuses do have stomachs, albeit unusual stomachs. In this paper I review the history of anatomical studies of the stomach of monotremes, discuss the functions of the stomach, and show how the absence of acid secretion has been confused with the absence of a stomach.

Historical

The platypus (Figure 1) is endemic to eastern Australia and Tasmania, and the first known European description and drawing was made by Governor John Hunter in 1797 (Nicol, 2018). The first descriptions of the internal anatomy of the platypus and echidna were made by

Everard Home in papers presented to the Royal Society; the platypus in December 1801 (Home, 1802a) and the echidna in June 1802 (Home, 1802b). Two platypuses and an echidna had been sent from New South Wales to Sir Joseph Banks, who then gave them to Home to examine. Home gave a detailed description of platypus anatomy, including the stomach, noting its small size: “*The stomach is a membranous bag, of an oval form, into which the oesophagus can hardly be said to enter, being rather continued along one end of the oval, till it forms the duodenum; so that the stomach appears to be a lateral dilatation of a canal, which is the oesophagus where the dilatation is formed, and becomes the duodenum immediately afterwards, at which part the coats are thickened, forming the valve of the pylorus. The stomach is smaller than in most other animals; in this respect it is like the true stomach of birds. In the collapsed state it is only 1½ inch [3.8 cm] long, and ¾ of an inch [1.9 cm] broad.*” Home also investigated the cheek pouches, likening them to those of monkeys. He described them as 1½ inch (3.8 cm) long and the same in breadth. Confusingly, after giving the dimensions of the stomach, he states “This is exactly double the size of one of the pouches in the cheek.”

Home (1802b) noted that in both the platypus and echidna the lining of the stomach was smooth and lacked glands for the secretion of acid or enzymes, the only secretory glands being Brunner’s glands in the most distal part of the stomach, which was confirmed later by detailed histological studies (Krause, 1970; Krause, 1971). Brunner’s glands are only found in mammals, usually in the proximal duodenum, and secrete mucins



Figure 1. Drawing of a platypus by Rachel Harris. Used by permission.

which in monotremes may provide protection from mechanical damage rather than the corrosive effects of acid and pepsin as in other mammals (Krause, 2000).

In his paper on the echidna, Home (1802b) commented on the differences between the echidna and platypus. “It is deserving of observation, that in this animal (the echidna), the mode of managing the food is different from that employed in the paradoxus (platypus); which accounts for the difference in the appearance of the teeth¹ and stomach. In this species, the food is bruised between the teeth placed upon the tongue and those of the palate; and immediately afterward the whole is conveyed into the stomach, and along with it a quantity of sand. The stomach therefore is sufficiently large to contain the food, and the extraneous matter connected with it; and it is defended from injury by its cuticular lining. In the paradoxus, the food is received into the mouth, is retained in two lateral pouches, and is prevented, by the two projecting teeth on the tongue, from getting into the stomach, till all the indigestible parts are separated; the nutritious matter alone being allowed to reach the stomach, which is of very small size.” The exact function of the “teeth” on the platypus tongue is still not entirely clear although Griffiths (1978) felt that it was “undoubtable” that they were concerned with transferring and directing the cheek pouch contents to the grinding pads, but Home’s insights were remarkable for someone who had never seen a live monotreme.

The science of comparative anatomy moved ahead rapidly in the 19th century. In 1805 Georges Cuvier published volume 3 of his monumental work “*Leçons d’anatomie comparée*” (Cuvier, 1805) which described the stomachs of nearly 100 mammals, as well as those of many birds, reptiles and fishes. Cuvier noted that some fish genera had no discernable stomach, while the platypus had a stomach, although it was very small. By contrast the echidna stomach was very large. In 1826 the great German anatomist Johann Meckel published a beautifully illustrated account of the anatomy of the platypus (Meckel, 1826). This was the first monograph on an Australian animal and included a figure showing the stomach (Figure 2). In 1897 Albert Oppel reviewed all published information on vertebrate stomachs in his monumental *Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbeltiere* (Textbook of Comparative Microscopic Anatomy of Vertebrates) (Oppel 1897), and concluded that the absence of gastric glands in the monotremes and some fish was due to secondary loss and was not an ancestral trait.

There are few published measurements of platypus stomach size. Home’s 3.81 cm x 1.9 cm was the first, while in his histological studies Krause gives the dimensions as 1.75 cm x 0.75 cm (Krause, 1971; Krause, 1975). Mackenzie (1918a) wrote that a stomach measuring 2.5 cm x 1.25 cm was the smallest he had seen while the largest was 6 cm x 3 cm. It is not surprising that there

¹ The keratinous tooth-like structures on the tongue and palate of the echidna and the mandible and maxilla of the platypus.

are differences in the estimates of stomach size as there are significant differences in the size on platypuses from different populations and significant differences between males and females (Nicol, 2013), and some stomachs may contain food. Despite the variations in estimated size, all the authors comment on the small size of the platypus stomach. Griffiths (1978) described it as “a very small stomach about the size of one’s little finger,” which would give it a volume of about 3 mL. Figure 2 shows a photograph of a platypus stomach next to Meckel’s 1826 illustration. It is small but is clearly distinguishable from the oesophagus and duodenum.

While platypus stomachs are small, those of echidnas are relatively large. In his monograph “Echidnas” (Griffiths, 1968) reported that a 3 kg echidna could ingest 200 g of termites in 10 minutes. This high rate of intake is made possible by the echidna’s sticky tongue and efficient processing in the mouth. In terms of volume of food in the stomach, that is comparable to a 75 kg human swallowing 5 kg of food in the same time. His later book “The Biology of Monotremes” (Griffiths, 1978) shows a photograph of the distended stomach of an echidna after such a meal, and it is by far the most obvious part of the gastrointestinal tract.

The many functions of the stomach

In most mammals there is a region of the stomach with cells that secrete hydrochloric acid and a precursor to the enzyme pepsin which together begin the breakdown of proteins. Most of the stomach lining contains cells which secrete mucus to protect against the corrosive mixture of acid and enzyme. Some mammals have a non-glandular region similar to the inside of our cheeks and the oesophagus (histologically described as stratified squamous epithelium) where the oesophagus enters the stomach. What is unique about monotreme stomachs is that they are entirely lined with stratified squamous epithelium, which means that they do not secrete acid and enzymes. Griffiths (1968) has described the absence of these glands from the stomach as a “monotreme specialization.”

Can we still call a stomach that does not secrete acid a stomach? Koelz (1992) gives this definition: “A true stomach is an enlargement of the lumen of the proximal gastrointestinal tract with a sphincter-like structure at its distal end”. Although the platypus does not have a distinct pyloric sphincter (Harrop and Hume, 1980), Home (1802a) felt that the thickening of the duodenum at its junction effectively formed the valve of the pylorus (see quote), and thus would slow emptying. A photographic sequence of a barium study on a conscious platypus (Booth and Connolly, 2008) shows a slightly distended stomach indicating that it would slow the movement of food from the oesophagus to the duodenum. With the exception of the monotremes and some amphibian larvae, vertebrate stomachs secrete hydrochloric acid and pepsin and most biology textbooks when discussing the stomach will concentrate on the role

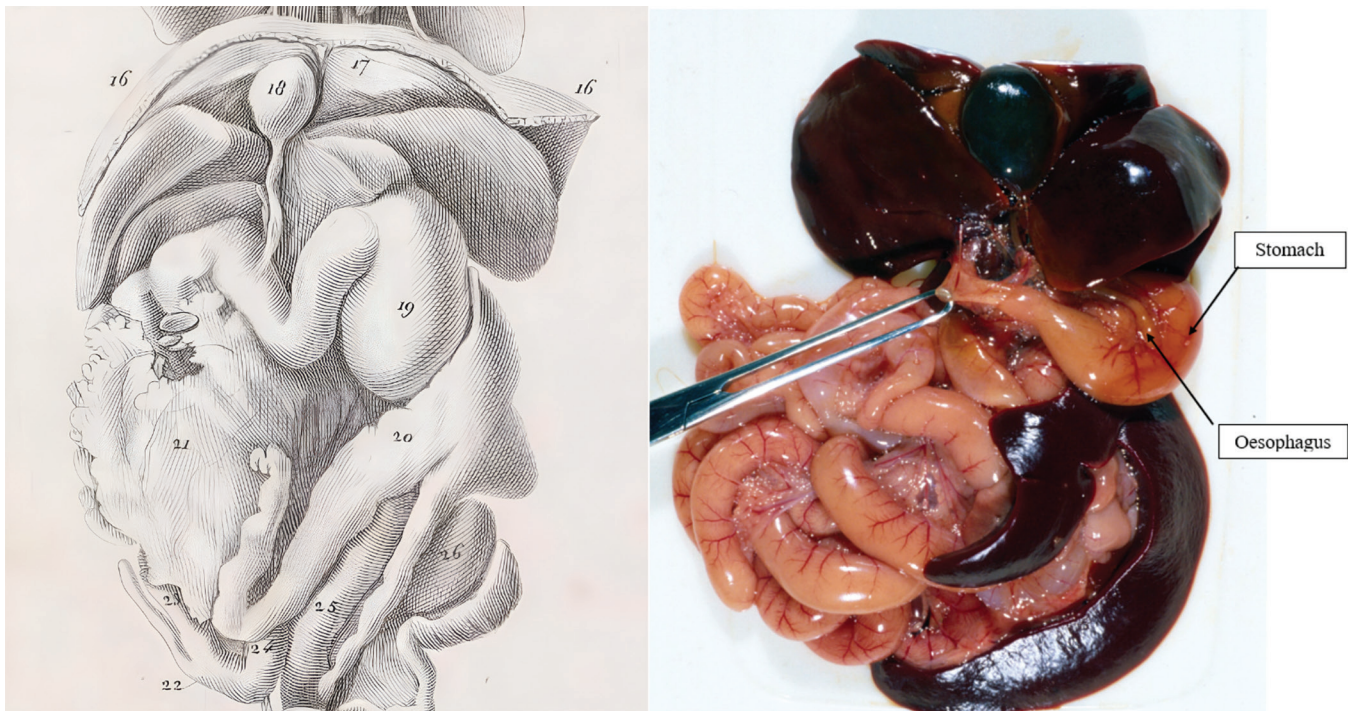


Figure 2. Abdominal organs of the platypus. Left, figure from *Ornithorhynchi paradoxi descriptio anatomica*, Meckel 1826; right, a photograph of the same area kindly provided by Joanne Connolly.

Key to labelling: 16 diaphragm, 17 liver, 18 gall bladder, 19 stomach, 20 spleen, 21 omentum 22 ileum, 23 colon, 24-25 rectum. The stomach sits between the liver and the large spleen. The photograph shows how narrow the oesophagus is. The forceps are holding the bile duct which enters the duodenum about 2.5 cm from the stomach. Assuming the gall bladder is about 2 cm long (Mackenzie, 1918b) the stomach in this photograph is about 3.5 cm long.

of these secretions in protein digestion. However, only 10 – 15% of protein digestion occurs in the stomach with most protein digestion and all absorption taking place in the small intestine (Koelz 1992). The basic function of the stomach is to store food and to continue the mechanical and chemical breakdown which may have begun in the mouth, and to release the resultant semifluid mass (chyme) into the duodenum at a rate that allows efficient digestion and absorption in the small intestine (Forte, 1996; Stevens and Hume, 1995). There now appears to be a consensus that the principal function of the acid gastric juice is not in protein digestion but to inactivate pathogenic microorganisms in the food and prevent them from reaching the small intestine (Martinsen *et al.*, 2019; Koelz, 1992; Beasley *et al.*, 2015) although it also facilitates absorption of iron, calcium and Vitamin B₁₂, as well as initiating protein digestion (Stevens and Hume, 1995; Koelz, 1992). Stomachs appeared early in vertebrate evolution - cyclostomes (lampreys and hagfish) do not have stomachs but sharks do, as do most later vertebrates (Stevens and Hume, 1995). As Cuvier noted, some teleost fish, both herbivorous and carnivorous, have no stomach, i.e. there is no stomach-like structure that can be distinguished anatomically or histologically (Castro *et al.*, 2014), and, to increase the chance of confusion, one of these is the pale chub *Zacco platypus*.

Platypus and echidnas do have stomachs, but unlike all other terrestrial vertebrates the stomachs of adult monotremes do not secrete acid. Why? One reason may

be that acid production in the stomach is a very energy intensive activity. The concentration of hydrogen ions in the acid secreted into our stomachs is about 2.5 million times the concentration in the blood. Pumping hydrogen ions against this enormous concentration gradient takes a lot of energy (Rong *et al.*, 1998). An acid-secreting stomach also must maintain barriers that protect the stomach from acid-related damage and concentrate bicarbonate and secrete it into the duodenum to neutralize the acid. Not secreting acid saves a lot of energy, and monotremes are characterized by low metabolic rates (Nicol, 2017). The echidna and platypus grind their invertebrate diet to a paste mixed with salivary secretions before it reaches the stomach, doing much of the work that is done in the stomach of other mammals (Griffiths, 1978). It is not clear how much chemical breakdown of food occurs in monotreme stomachs, but it is likely there is some self-digestion by enzymes inside the gastrointestinal tracts of the invertebrate prey which are released when the food is ground up, some digestion of carbohydrates by salivary enzymes, and probably some breakdown by stomach microbes, which would be facilitated by the absence of stomach acid, but the majority of chemical digestion occurs in the small intestine where proteins, fats and carbohydrates are broken down by enzymes secreted by the pancreas in an alkaline environment provided by the bicarbonate in the pancreatic fluid (Griffiths, 1978).

The importance of the stomach in storing food and regulating its release into the small intestine can be seen in human patients whose stomach has been surgically removed. They are able to maintain a normal nutritional status, but the loss of the storage capacity of the stomach means they must eat frequent small meals to avoid the unpleasant effects of rapid gastric emptying known as dumping syndrome (Ryu, 2022). These patients also illustrate a less well appreciated function of the stomach: it is essential for Vitamin B₁₂ absorption. Without B₁₂ supplements they will develop lethal megaloblastic anemia. Vitamin B₁₂ (also known as cobalamin) is required for red cell production and its absorption in the ileum depends on it being bound to intrinsic factor, a glycoprotein produced by the acid-secreting cells in the stomach. Koelz (1992) notes that synthesis and secretion of intrinsic factor is the only indispensable function of the stomach in humans. This is not a problem for monotremes as they produce intrinsic factor in the pancreas and secrete it into the duodenum, as do some other mammals, including dogs (Ordoñez *et al.*, 2008).

The genetic origins of gastric confusion

So, back to the quote I began with, from an article (Yong, 2013) which was on-line shortly before the paper to which it refers (Castro *et al.*, 2014) was formally published. Castro *et al.* (2014) investigated the genes associated with the loss of acid secretion in stomach-less fish and compared this with the loss of these genes in the platypus, which had been described some years previously (Ordoñez *et al.*, 2008). Castro *et al.* (2014) initially discussed “the lack of a stomach phenotype (acid secretion and pepsin activity)”, but then referred to “the stomach-less mammal, the platypus.” Ordoñez *et al.* (2008) refer many times to the platypus stomach but describe it as being non-functional - implying that the only function of a stomach is acid-based digestion. The absence of acid secretion has become equated with the absence of a stomach, ignoring the other functions of a stomach, and despite there being many anatomical descriptions of the stomachs of both monotremes. Even the eutherian giant anteater (*Myrmecophaga tridactyla*) has been caught up in this misunderstanding, presumably on the assumption that all anteaters must be the same. According to the University of Edinburgh’s natural history collection web page on the Family Myrmecophagidae (Blaxter and Stone, 2024) “An anteater’s stomach does not produce hydrochloric acid, but instead relies on the formic acid produced by the prey to help with digestion.” This claim is also made on Wikipedia (2024) and the websites of a large number of zoos and similar institutions. Giant anteaters, silky anteaters and tamanduas have a relatively simple stomach but within it there is an area with acid-secreting glands, and the pyloric area of the stomach before it empties into the duodenum is quite unlike the monotreme stomach (Stevens and Hume, 1995). In the giant anteater this area has thick walls and is extremely

muscular and resembles the gizzard of a bird, implying that as well as acid digestion there is much more mechanical breakdown of food in the stomach of Myrmecophaga than in the stomach of monotremes. Digestion of food by the formic acid in the prey seems extremely unlikely. The tiny amounts of formic acid, at most a few milligrams per ant (O’Rourke, 1950), would be quickly neutralised by the copious bicarbonate rich secretions from the large salivary glands that are characteristic of ant-eating mammals. Perhaps more importantly, although formic acid was named after the Latin for ant (formica) only one subfamily of ants, the Formicinae produces formic acid (O’Rourke, 1950). Giant anteaters, like other anteaters including the echidna (Sprent and Nicol, 2016), eat ants from a wide range of subfamilies, and in some habitats they feed nearly exclusively on termites (Santana *et al.*, 2024), which do not produce formic acid.

Conclusions and final questions

In his description of the platypus gastrointestinal system (Mackenzie, 1918a) wrote ‘*The stomach of the platypus presents a somewhat primitive type...*’ Up until quite recently any features of monotremes that differed from an anthropocentric eutherian model was considered as evidence of their primitivity, but now it seems that any departures from this same model are likely to be described as weird or bizarre. This clickbait approach to popular science can have the same effect as casting all aspects of the deviation of monotremes from the therian model as primitive: it discourages thoughtful analysis and leads to an underappreciation of the elegance of adaptive evolution. In some cases it seems to encourage the invention of false facts to “sex up” the story and this raises a much more general question about where non-scientists and even non-specialists can get reliable information on specific topics.

Two questions arise from the above discussions: firstly, if gastric acidity is so important in protecting against pathogenic microorganisms taken in with food that most vertebrates, including all other mammals, maintain this energetically expensive defence, how are monotremes able to cope without it? This has quite wide ramifications into the evolution and role of gastric acidity, and an analysis of the relationship between gastric acidity and trophic group has demonstrated that scavengers and carnivores have significantly higher stomach acidities compared to herbivores or carnivores feeding on phylogenetically distant prey such as invertebrates or fish (Beasley *et al.*, 2015). This is a promising lead but something I will not attempt to further explore here.

The other question is why is the platypus stomach so small? Harrop and Hume (1980) suggest that the presence of the grinding pads and cheek pouches may be an explanation and Home’s (1802a) insights into platypus feeding appear to have been on the right track. Feeding behaviour of the platypus is unlike that of any other

mammal. Like echidnas, they are toothless, but unlike echidnas or any other toothless mammal, they masticate their food (Hayashi *et al.*, 2024). Instead of molars, platypus have keratinous pads on the maxilla and lower jaws, and cheek pouches, each comparable in size to the stomach, immediately adjacent to these pads (see Plate 3 in Home (1802a) and Figure 6.3 in Booth and Connolly (2008)). Platypuses use their bill to collect a wide range of invertebrates from the bottom of streams, rivers and ponds, storing them in the cheek pouches while they remain under water. When they surface they masticate their food very finely using their keratinised pads and exoskeletons are sifted out and removed before swallowing (Booth and Connolly, 2008). Platypus prey items are so finely ground before they enter the stomach that they are

unrecognizable, so that platypus diet studies use samples from the cheek pouches (Faragher *et al.*, 1979). The mixing and maceration that normally occurs in mammal stomachs has already occurred. Storing food in the cheek pouches, immediately adjacent to the masticatory pads where it is reduced to a fine slurry with most indigestible material removed, may have made the stomach much less important, and led to a reduction in its size, but the organ that remains is still a stomach.

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